Life history responses of meerkats to seasonal changes in extreme environments

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Title: Life-history responses of meerkats to seasonal changes in extreme environments

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Abstract:

Species in extreme habitats increasingly face changes in seasonal climate, but the demographic mechanisms through which these changes affect population persistence remain unknown. We investigated how changes in seasonal rainfall and temperature affected vital rates and viability of an arid-environment specialist, the Kalahari meerkat, through effects on body mass. We show that climate change reducing adult mass in the pre-breeding season would decrease fecundity during the breeding season and increase extinction risk, particularly at low population densities. In contrast, a warmer non-breeding season resulting in increased mass and survival would buffer negative effects of reduced rainfall during the breeding season, ensuring persistence. As most ecosystems are seasonal, a full understanding of species vulnerability to global change relies on linking seasonal trait and population dynamics.

One Sentence Summary:

Trait-mediated survival and reproduction determine population persistence under seasonal changes in extreme rainfall and temperature

Main Text:

Ecosystems subject to climatic extremes, such as arid regions, which cover > 40 % of the terrestrial landmass, are among the most vulnerable to climate change (*1–3*). Changes in rainfall-drought cycles (*2*, *4*) and increasing temperatures (*5*) are likely to severely affect population dynamics of arid-environment species (*6*). This is because key vital rates, such as survival, growth, and reproduction, of these species respond unusually strongly to seasonal and interannual climatic patterning (*2*, *5*, *7*). Despite this increased vulnerability, population viability analyses of arid-environment specialists are scarce (*6*). Studies on seasonal changes in vital rates and phenotypic traits, which strongly mediate climatic effects on viability (*8–10*), are thus far absent.

In this study, we used long-term demographic and trait (body mass) data of meerkats (*Suricata suricatta*) from the Kalahari desert in southern Africa to investigate how future changes in seasonal rainfall and temperature may affect vital rates and population persistence. Meerkats are an ideal study species since vital rates can be measured precisely (*11*) and respond strongly to climatic factors, generating large variation in population size (*8*, *12*). In addition, meerkats are cooperative breeders, where young born to a dominant female are co-reared by non-breeding helpers (*13*), and the number of helpers in the population increases reproductive success (*8*, *14*). This relationship allows us to assess how interactions between population density and climate affect vital rates (*12*, *15*). To establish a basis for detailed projections of population

change over time, we first used 20 years of individual data from female meerkats to fit generalized additive models (GAMs) (*8*). In these models, vital rates (survival, growth, reproduction, stage transitions, and emigration) of nine life-history stages (pups, juveniles, subadults, and non-pregnant, pregnant, and litter-weaning helpers and dominants; fig. S1) were fitted as functions of body mass, population density, season (month-of-year), interannual rainfall and temperature deviations (from seasonal means), and interactions among these drivers (*8*) (Table S1).

Our results from the most parsimonious GAMs agreed with previous findings, showing strong seasonal effects, both positive and negative, of all considered variables on meerkat vital rates (*8*, *12*). For instance, monthly growth in adult helpers was generally highest ($P < 0.01$) in the rainy season when food resources were most abundant (Fig. 1A). Interactions between population density and rainfall/temperature deviation mediated these seasonal effects. High density and rainfall increased helpers' growth (Fig 1A). High density under low temperatures however decreased the probability of dominant reproduction at the onset of the dry season (Apr-May) (Fig 1B). Overall, body mass had a consistently positive effect on vital rates, strongly mediating environmental impacts (*8*). Rainfall also positively affected vital rates (*12*, *16*), whereas the effect of higher temperatures was positive only in dry and cool seasons (Apr-Aug) (Table S2, fig. S18). Under most environmental conditions, population density showed a negative effect on survival and on emigration of adult helpers (*12*). In dominants, however, survival increased with density at the onset of the breeding season but decreased at high densities in the non-breeding season, when resources were scarce. Highest reproductive output was achieved at intermediate densities (Table S2). Population density therefore both amplified and

compensated negative responses to the environment, depending on the vital rate affected (*15*) (Fig. 1).

We next assessed how changes in climate variation across seasons might affect population dynamics through direct effects on vital rates and through effects mediated by body mass and density. We first used the most parsimonious GAMs of vital rates to assemble a density-dependent, environment-specific, mass-stage classified integral projection model for each study month and year (*17*; supplementary materials). This enabled us to project trait and population dynamics simultaneously in discrete one-month intervals, which could then be integrated over the entire year (fig. S2). Our population model assumed that past conditions affecting meerkats were captured by the current mass distribution and were propagated through time, allowing us to assess trait-mediated population processes (*10*). These assumptions were justified as we could not detect life-history tradeoffs (*i.e.*, fitness decreases due to high growth or reproductive effort; supplementary text) (*16*).

The population model replicated observed seasonal population and mass fluctuations (1997-2016) with high accuracy (for total population density: Pearson's correlation coefficient $r = 0.74$, $P < 0.001$) (Fig.1B), and did not extrapolate beyond biologically realistic values of masses (figs. S3 and S4). Model projections were also robust, showing low uncertainty due to parameter estimates (Tables S3 and S4). We then used this model to project population dynamics for 50 years based on 12 scenarios of changes in rainfall (drier) and temperature (hotter) extremes. These scenarios were derived from four projections of greenhouse-gas emissions, showing a plausible range of season-specific climate change in the Kalahari (figs. S5 and S6).

Projected changes in climatic patterning, and increases in extreme events in particular, increased the risk of population quasi-extinction (< 20 individuals or < 5 dominants) up to 55 %

by 2066 (Fig. 2A, B). Simultaneous changes in rainfall and temperature led to a higher extinction risk (figs. S7 and S8), highlighting potentially detrimental compound climate-change effects on the viability of arid-environment species (*18*). Density was important in regulating persistence (Fig. 2C); projections that kept populations at either low or high densities resulted in significantly higher probability of quasi-extinction (to 100 %, $P < 0.01$) and decreased time to extinction on average by 20 years (SE = 10; $P < 0.01$). At low population densities, when the benefits of cooperation decrease and the environment favors the settlement of new groups (*12*, *19*), emigration was relatively high. This reduced both the overall number of helpers and reproductive success (*20*; fig. S14). At high densities, when resource competition and intergroup conflicts increase, particularly under scarce rainfall (Table S2), reproduction and survival were reduced, increasing the risk of extinction (*21*). Maintaining densities at intermediate levels, when the benefits of cooperation are largest, eliminated extinction risk (Fig. 2C), similar to patterns seen in other social species (*20*).

As well as influencing viability, projected changes in climate significantly altered population structure due to changes in the distribution of mass. In projections where climatic extremes became more likely but the population persisted, the proportion of non-pregnant dominant females increased (compared to baseline simulations) at the end of the breeding season (Apr-Jul); as well as the proportion of pregnant dominant females and of females with dependent litters at the onset of the breeding season (Aug-Nov; Fig 3A). This occurred due to mass increases of helpers (from 600 to up to 670 grams) and dominants in the dry season (May-Sep; Fig. 3B), which led to higher reproductive output in subsequent months and compensated for the loss of adult helpers from the population (Fig. 3A). These changes in the proportion of helpers and dominants indicate a reduction in average group size under climate change (*21*). In contrast,

in projections where the population collapsed, the proportion of non-pregnant helpers dropped to 20 % (from 40 % in baseline simulations), as helpers emigrated more readily under low population densities (Fig. 3). Density was further reduced by a lower reproductive output that resulted from decreased masses of reproductive females at the onset of the breeding season (Fig. 3B), providing a potential early-warning signal for an impending population crash (*22*). Therefore, for social species, in particular cooperative breeders, density feedbacks (*23*) may exacerbate a breakdown of social groups under climate change (*21*).

To explore the seasonal demographic mechanisms behind projected quasi-extinctions, we assessed how perturbations of our population model affected population growth. We replicated simulations which had resulted in extinction but maintained the effects of rainfall and temperature deviations at observed past values (1997-2016) for either specific vital rates or simultaneously for all vital rates, accounting for covariation (fig. S11). We maintained the effects either for the entire year or across four seasons: rainy (Oct-Apr), dry (May-Sep), hot (Nov-Feb), and cool (Jun-Aug). Our results demonstrate highly season-specific contributions of demography to extinction. The time to extinction can be slowed by 4 years on average (SE = 2.1) if the reproduction of dominants is not affected by climate change in the rainy season (Fig 4; Fig. S10). On the other hand, increasing warming can potentially decrease emigration, particularly in the dry and cool seasons, despite potential mass gains of prospective emigrants. Maintaining emigration under observed rainfall and temperature regimes therefore leads to faster extinction (Fig. 4). These results agreed with analytical perturbations of population growth, which showed high but seasonally varying relative contributions of helper and dominant vital rates to population growth (figs. S12 and S13).

This work highlights that assessing the dynamics of seasonal influences on phenotypic traits may be key to understanding how changes in demography and population structure can ensure population persistence when rainfall and temperature patterns change (*5*, *10*). In particular, we show that climate-driven changes in body mass affect vital rates differently in different seasons. These trait-mediated effects can either buffer populations from extinction (*15*) or exacerbate extinction risk under climate-density interactions for species where density positively affects vital rates (*15*, *24*). Seasonal, demographic analyses that include phenotypic-trait changes are therefore required to gain much-needed information on population responses to global change, such as interactions of climatic components that are increasingly extreme (*18*, *24*, *25*).

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Author Contributions: T.C.B. led the long-term study and data collection; M.P. and A.O. conceived the ideas for the paper and its structure; M.P., A.O., N.M. and G.C. designed the analyses; M.P. conducted the analyses and wrote the manuscript; all authors discussed the results and commented on the manuscript.

Competing interests: The authors have no competing interests to declare.

Data and materials availability: The parameters and datasets generated and analyzed during the current study, required to build and project meerkat population dynamics are freely available in the *GitHub* repository: https://github.com/MariaPaniw/meerkats. All analyses in this study were performed using the freely available, statistical software *R*. All R script to run the analyses are available in the *GitHub* repository: https://github.com/MariaPaniw/meerkats. All correspondence and material requests should be addressed to M. Paniw at m.paniw@gmail.com.

Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S17

Tables S1 to S4

Caption for Fig. S18

Captions for R scripts S1 to S3

Captions for databases S1 to S17

References (*26-57*)

Figures:

Figure 1. Interactive effects of seasonality, population density, and rainfall/temperature variation on meerkat vital rates and population dynamics. (A) Line colors and different plot panels depict predictions of body mass (g) and reproduction using maximum (+) and minimum (-) observed temperature and rainfall deviation from seasonal averages, respectively. Shaded areas show 95% prediction intervals. Plot backgrounds highlight the rainy (Oct-Apr) and dry (May-Sep) seasons. (B) Average (lines) ± 95% bootstrap confidence intervals (shaded areas) projected

299 population densities (individuals/km^2) obtained from modeling the relationships described in
300 (A).

301 **Figure 2. Projected density and viability of meerkats under changes in rainfall and**
302 **temperature variation.** (A) Average (lines) population density (individuals/km^2) ± 95%
303 projection interval (shaded areas) based on 280 and 120 simulations where the population
304 persisted or went extinct, respectively. (B) Cumulative probabilities of quasi-extinction under
305 four scenarios of greenhouse-gas Representative Concentration Pathways (RCPs). Shaded areas
306 show 95 % projection intervals among sequential vs. stochastic projections of climate. (C)
307 Effects on extinction probability of imposing constant low, intermediate, and high densities
308 during projections. Plot backgrounds highlight the rainy (Oct-Apr) and dry (May-Sep) seasons.

309 **Figure 3. Projected changes in population structure and trait dynamics for meerkats under**
310 **climate change.** Seasonal distribution of proportion of different life-history stages (A) and
311 average masses (g) within each stage (B). Boxplots show the distribution of values across years
312 and simulations grouped based on different simulations of future rainfall and temperature
313 variation. The stages include pups, juvenile (Juv), subadults (SubA), and non-pregnant (NP),
314 pregnant (P) and litter-weaning (L) helpers (H) and dominants (D). Plot backgrounds highlight
315 the rainy (Oct-Apr) and dry (May-Sep) seasons.

316 **Figure 4. Seasonal differences in probability of quasi-extinction under climate-change**
317 **simulations.** Averages (points) ± 1 SE (error bars) changes in the time (years) to extinction
318 across 120 simulations when a given vital rate is affected by observed (1997-2016), instead of
319 projected (2017-2066), rainfall/temperature variation. The observed variation was maintained
320 over an entire year or for the rainy (Oct-Apr), dry (May-Sep), hot (Nov-Feb) or cool (Jun-Aug)
321 seasons.

Figure 1

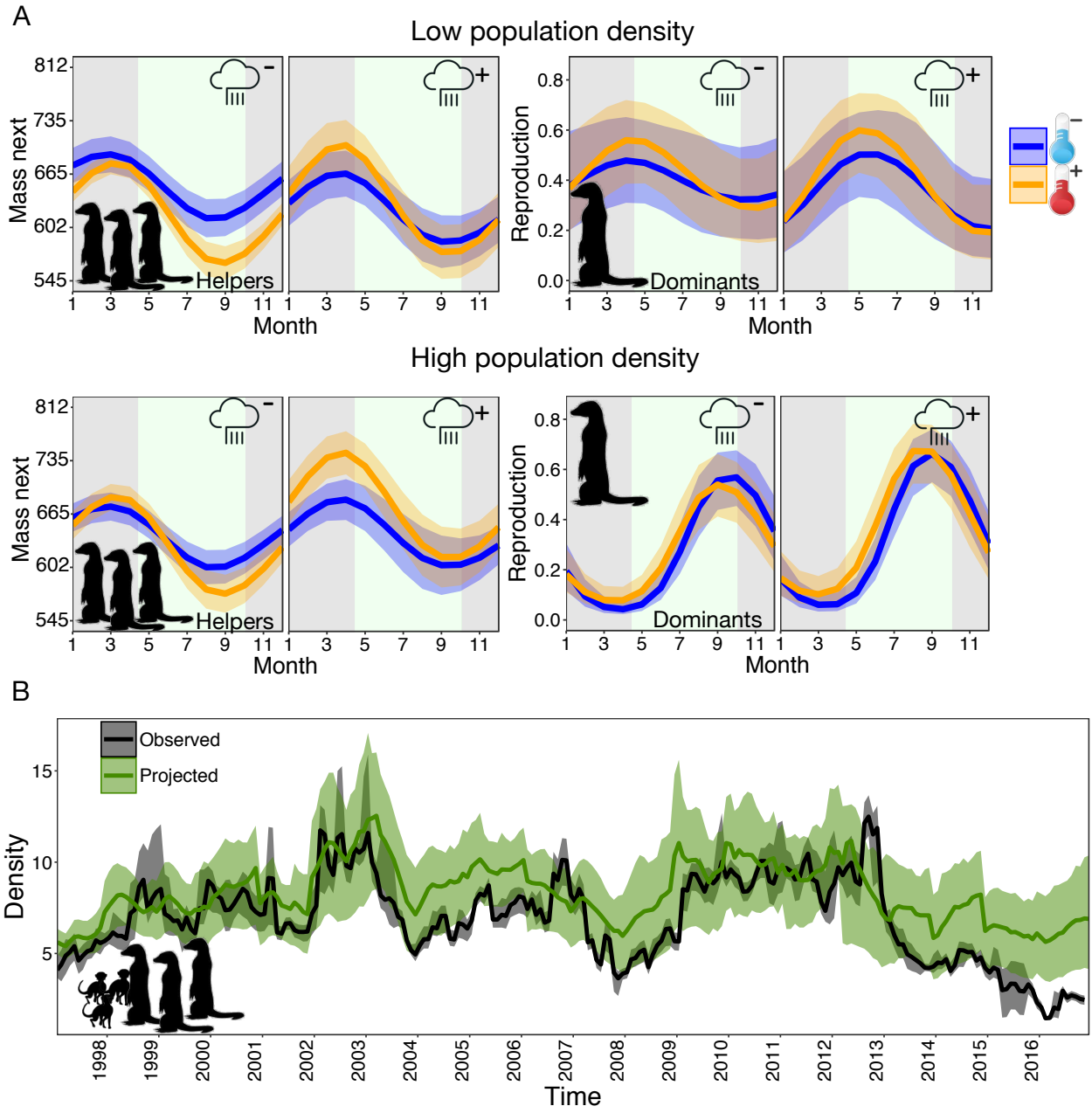
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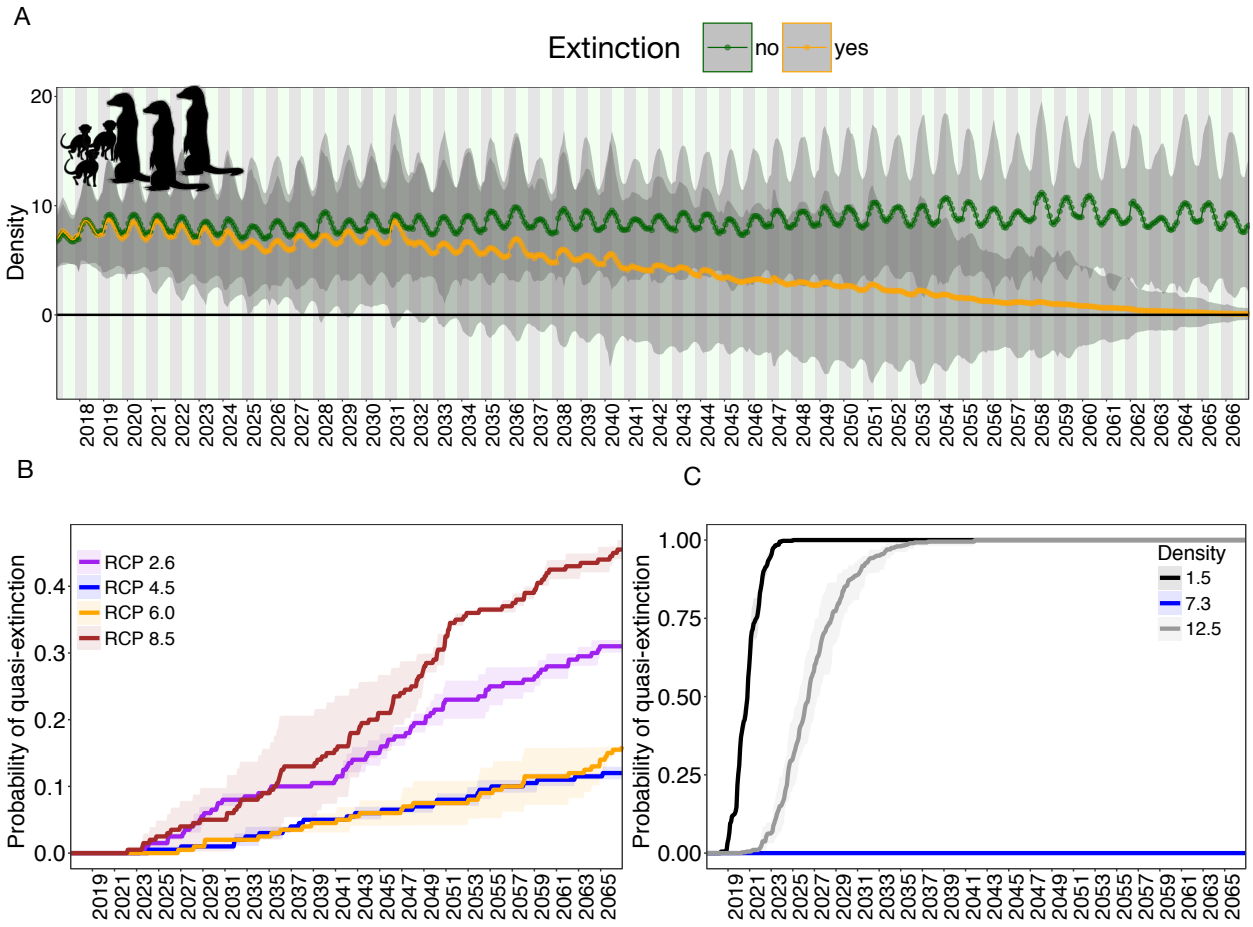
Figure 2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B
Probability of quasi-extinction
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RCP 4.5
RCP 6.0
RCP 8.5
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C
Probability of quasi-extinction
Density
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Figure 3

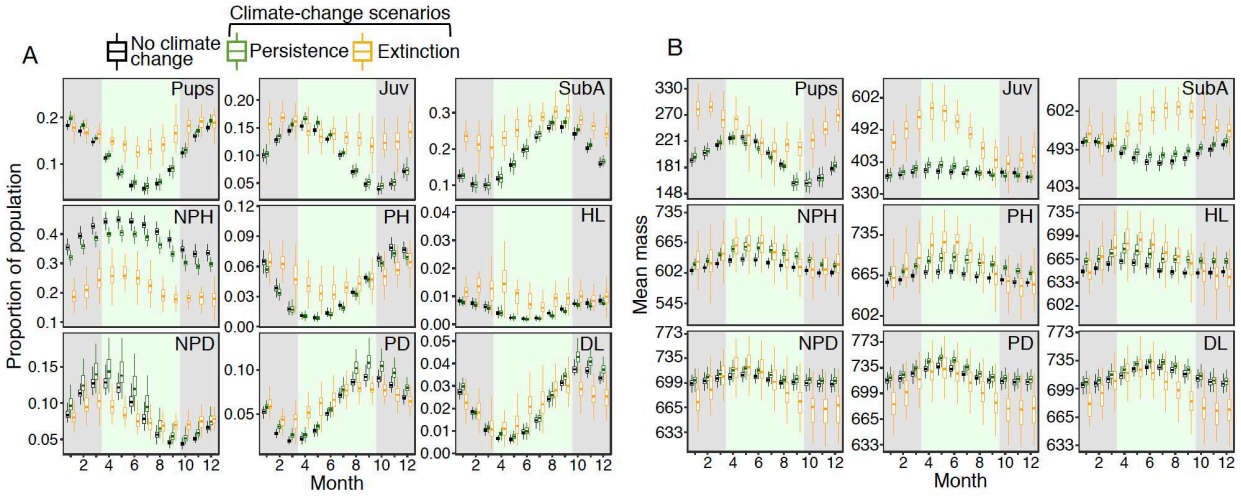

Figure 4